

REPORT DOCUMENTATION PAGE			Form Approved OMB NO. 0704-0188		
<p>The public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington VA, 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to any penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number.</p> <p>PLEASE DO NOT RETURN YOUR FORM TO THE ABOVE ADDRESS.</p>					
1. REPORT DATE (DD-MM-YYYY) 10-11-2014		2. REPORT TYPE Final Report		3. DATES COVERED (From - To) 1-Aug-2013 - 31-Jul-2014	
4. TITLE AND SUBTITLE Final Report: Investigating Maneuverability, Stability and Control of Flapping Flight			5a. CONTRACT NUMBER W911NF-13-1-0275		
			5b. GRANT NUMBER		
			5c. PROGRAM ELEMENT NUMBER 611102		
6. AUTHORS Itai Cohen, Tsevi Beatus			5d. PROJECT NUMBER		
			5e. TASK NUMBER		
			5f. WORK UNIT NUMBER		
7. PERFORMING ORGANIZATION NAMES AND ADDRESSES Cornell University 373 Pine Tree Road Ithaca, NY 14850 -2820			8. PERFORMING ORGANIZATION REPORT NUMBER		
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS (ES) U.S. Army Research Office P.O. Box 12211 Research Triangle Park, NC 27709-2211			10. SPONSOR/MONITOR'S ACRONYM(S) ARO		
			11. SPONSOR/MONITOR'S REPORT NUMBER(S) 61651-EG.2		
12. DISTRIBUTION AVAILABILITY STATEMENT Approved for Public Release; Distribution Unlimited					
13. SUPPLEMENTARY NOTES The views, opinions and/or findings contained in this report are those of the author(s) and should not be construed as an official Department of the Army position, policy or decision, unless so designated by other documentation.					
14. ABSTRACT Due to aerodynamic instabilities, stable flapping flight requires ever-present fast corrective actions. We investigated how flies control body roll angle, which is unstable and their most sensitive degree of freedom. We glued a magnet to each fly and applied a short magnetic pulse that rolls it in mid-air. Fast video shows flies correct perturbations up to 100 degrees within 30ms by applying a stroke-amplitude asymmetry that is well described by a linear PI controller. For more aggressive perturbations, we show evidence for nonlinear and hierarchical control mechanisms. Flies respond to roll perturbations within 5ms, making this correction reflex one of the fastest in the					
15. SUBJECT TERMS Insect flight, flight control,					
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT UU	15. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON Itai Cohen
a. REPORT UU	b. ABSTRACT UU	c. THIS PAGE UU			19b. TELEPHONE NUMBER 607-255-0815

Report Title

Final Report: Investigating Maneuverability, Stability and Control of Flapping Flight

ABSTRACT

Due to aerodynamic instabilities, stable flapping flight requires ever-present fast corrective actions. We investigated how flies control body roll angle, which is unstable and their most sensitive degree of freedom. We glued a magnet to each fly and applied a short magnetic pulse that rolls it in mid-air. Fast video shows flies correct perturbations up to 100 degrees within 30ms by applying a stroke-amplitude asymmetry that is well described by a linear PI controller. For more aggressive perturbations, we show evidence for nonlinear and hierarchical control mechanisms. Flies respond to roll perturbations within 5ms, making this correction reflex one of the fastest in the animal kingdom.

Enter List of papers submitted or published that acknowledge ARO support from the start of the project to the date of this printing. List the papers, including journal references, in the following categories:

(a) Papers published in peer-reviewed journals (N/A for none)

<u>Received</u>	<u>Paper</u>
-----------------	--------------

TOTAL:

Number of Papers published in peer-reviewed journals:

(b) Papers published in non-peer-reviewed journals (N/A for none)

<u>Received</u>	<u>Paper</u>
-----------------	--------------

TOTAL:

Number of Papers published in non peer-reviewed journals:

(c) Presentations

KNAW Biophysics Meeting, Netherlands (2014)
Experimental Chaos and Complexity, Scotland (2014)

Number of Presentations: 2.00

Non Peer-Reviewed Conference Proceeding publications (other than abstracts):

Received Paper

TOTAL:

Number of Non Peer-Reviewed Conference Proceeding publications (other than abstracts):

Peer-Reviewed Conference Proceeding publications (other than abstracts):

Received Paper

TOTAL:

Number of Peer-Reviewed Conference Proceeding publications (other than abstracts):

(d) Manuscripts

Received Paper

11/10/2014 1.00 Tsevi Beatus, John Guckenheimer, Itai Cohen. Roll Control in Fruit Flies, Royal Society Interface Focus (11 2014)

TOTAL: 1

Number of Manuscripts:

Books

Received Book

TOTAL:

Received Book Chapter

TOTAL:

Patents Submitted

Patents Awarded

Awards

Graduate Students

<u>NAME</u>	<u>PERCENT_SUPPORTED</u>
FTE Equivalent:	
Total Number:	

Names of Post Doctorates

<u>NAME</u>	<u>PERCENT_SUPPORTED</u>
Tsevi Beatus	1.00
FTE Equivalent:	1.00
Total Number:	1

Names of Faculty Supported

<u>NAME</u>	<u>PERCENT SUPPORTED</u>	National Academy Member
Itai Cohen	0.00	No
John Guckenheimer	0.00	
FTE Equivalent:	0.00	
Total Number:	2	

Names of Under Graduate students supported

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
FTE Equivalent:	
Total Number:	

Student Metrics

This section only applies to graduating undergraduates supported by this agreement in this reporting period

The number of undergraduates funded by this agreement who graduated during this period: 0.00

The number of undergraduates funded by this agreement who graduated during this period with a degree in science, mathematics, engineering, or technology fields:..... 0.00

The number of undergraduates funded by your agreement who graduated during this period and will continue to pursue a graduate or Ph.D. degree in science, mathematics, engineering, or technology fields:..... 0.00

Number of graduating undergraduates who achieved a 3.5 GPA to 4.0 (4.0 max scale):..... 0.00

Number of graduating undergraduates funded by a DoD funded Center of Excellence grant for Education, Research and Engineering:..... 0.00

The number of undergraduates funded by your agreement who graduated during this period and intend to work for the Department of Defense 0.00

The number of undergraduates funded by your agreement who graduated during this period and will receive scholarships or fellowships for further studies in science, mathematics, engineering or technology fields: 0.00

Names of Personnel receiving masters degrees

<u>NAME</u>
Total Number:

Names of personnel receiving PHDs

<u>NAME</u>
Total Number:

Names of other research staff

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
FTE Equivalent:	
Total Number:	

Sub Contractors (DD882)

Inventions (DD882)

Scientific Progress

Technology Transfer

We have spoken about our work at various government agencies including the Army and Airforce.

Fast roll control in fruit flies: evidence for a nonlinear response mechanism

Tsevi Beatus¹ John M. Guckenheimer², and Itai Cohen¹

Departments of ¹Physics and ²Mathematics, Cornell University, Ithaca, New York 14853, USA

(Dated: November 10, 2014)

Statement of the problem studied:

Due to aerodynamic instabilities, stable flapping flight requires ever-present fast corrective actions. Here we investigate how flies control body roll angle, which is unstable and their most sensitive degree of freedom. We glue a magnet to each fly and apply a short magnetic pulse that rolls it in mid-air. Fast video shows flies correct perturbations up to 100° within $30 \pm 7\text{ms}$ by applying a stroke-amplitude asymmetry that is well described by a linear PI controller. For more aggressive perturbations, we show evidence for nonlinear and hierarchical control mechanisms. Flies respond to roll perturbations within 5ms, making this correction reflex one of the fastest in the animal kingdom.

Summary of the most important results:

Locomoting organisms evolved mechanisms to control their motion and maintain stability against mechanical disturbances. The control challenge is prominent in small flying insects since their small moment of inertia renders them susceptible even to gentle air currents [1–4]. Moreover, they fly at Reynolds numbers $\text{Re} = 10^2 - 10^4$, in which flows are unsteady [5, 6]. Most importantly, flapping flight is aerodynamically unstable, on a time scale of a few wing-beats [7–18]. It is, therefore, intriguing how insects overcome such control challenges and manage to fly with impressive stability, maneuverability and robustness, outmaneuvering any man-made flying device.

Among the body Euler angles – yaw, pitch and roll – roll is most sensitive to perturbing torques since the moment of inertia of the insect’s long axis is smallest [1, 2]. Recent fluid dynamics simulations suggest roll is *unstable* due to an unsteady aerodynamic mechanism, where it is positively coupled to sideways motion via asymmetry of the leading-edge vortex attached to each wing [14–18]. Such results indicate flies can lose their body attitude due to roll perturbations within 4 wing-beats. Controlling roll is also crucial for maintaining direction and altitude. Thus, any basic understanding of insect flight demands quantitative analysis of roll control.

Previous studies used tethered animals to measure response to imposed roll rotations [19–24] and visual roll stimuli [23–29]. In such experiments, however, the tethered insect does not control its motion and often exhibits wing kinematics and torques qualitatively different from those in free-flight [30, 31]. More recently, free-flight experiments used vortices [1–3] and impulsive gusts [4] to perturb insects, highlighting the sensitivity of the roll angle to perturbations. Understanding roll control however, requires fast and accurate quantitative measurements of wing and body kinematics in response to controlled mid-air perturbation impulses – a methodology recently applied to study yaw control [32]. Crucially, these previous works typically consider only the linear response [29, 32–38]. Whether non-linear mechanisms come into play in natural free flight, where both large and coupled perturbations are common [1] remains unknown.

Here, we perturb a fruit-fly (*Drosophila melanogaster*) by gluing a magnet to its back and applying a $\sim 5\text{ms}$ magnetic pulse that rolls it in mid-air. The perturbation amplitude ranges from roll deflections of 5° to multiple rotations along roll. We use high speed video to film the fly’s corrective maneuver and measure its wing and body kinematics [39]. We find that for roll perturbations up to 70° flies generate corrective torques by applying a stroke-amplitude asymmetry that is described by the output of a linear PI controller for roll. The asymmetry starts only one wing-beat ($\sim 5\text{ms}$) after the perturbation onset, making the roll correction reflex one of the fastest in the animal kingdom [40]. Surprisingly, however, we find that linear control is *not* sufficient to explain the response for multiple rotations nor the overarching control structure for simultaneously handling yaw, pitch, and roll.

To exert mid-air mechanical perturbations along roll we glue a magnetic pin, 1.5 – 2mm long, to the dorsal thoracic surface of each fly (Fig. 1). The pin is oriented horizontally and perpendicular to the body axis. In each experiment ~ 15 flies are released in a transparent chamber equipped with two Helmholtz coils that are used to generate a vertical magnetic field ($\sim 10^{-2}\text{Tesla}$). When a fly crosses the filming volume, a laser-trigger initiates video recording at $8000\text{ frames s}^{-1}$ along three orthogonal axes, as well as a 5ms (1 wing beat) magnetic pulse [32, 39]. Since fruit flies fly with their body axis pitched up at $\sim 45^\circ$ and since the moment of inertia along their body axis is ~ 4 times smaller than the other axes, the largest deflection is generated along the body roll axis, with smaller perturbations along pitch and yaw (Fig. 1a,b). Using a custom image analysis algorithm [39], we extract a 3D kinematic description of the fly (Fig. 1) consisting of its body position and orientation (Fig. 1b) as well as the Euler angles (Fig. 1c) for both wings (see Supplementary Information (SI)). We analyzed 20 sequences that span a perturbation range between 5° and 100° , in which the flies perform a steady flight before and after the correction maneuver.

A representative example of a fly recovering from a 60° roll perturbation is shown in Fig. 1 and Movie 1. Body Euler angles, roll (ρ), yaw (ϕ_b) and pitch (θ_b) are plotted in Fig. 1e. The magnetic field was applied be-

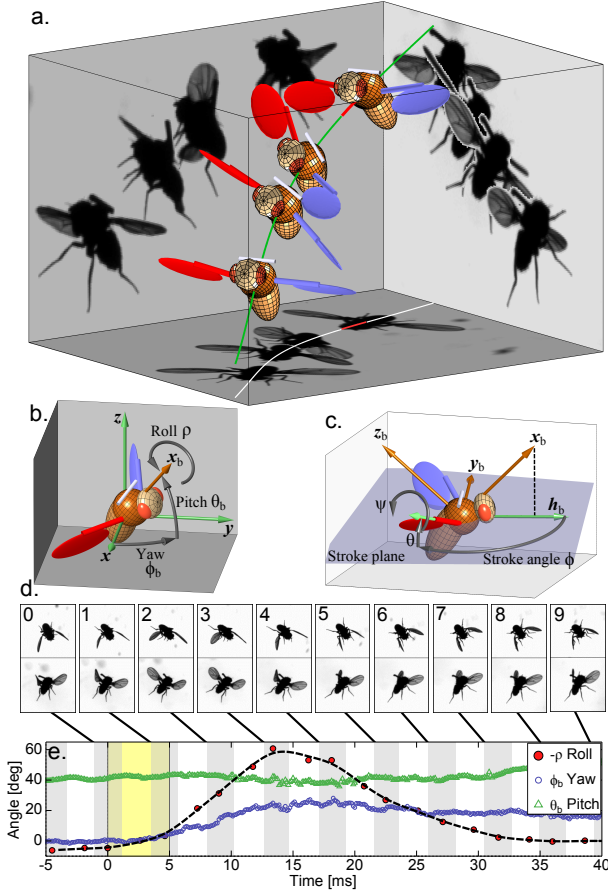


FIG. 1. Roll perturbation and correction: (a) Images from 3 orthogonal cameras of a roll perturbation and correction maneuver. Each panel shows 4 superposed images. The 3D-rendered fly represents the kinematic data of the body and wings. The perturbation location (red line) is shown on the fly's center-of-mass trajectory (green). In the second snapshot the fly is rolled 60° to its left. (b) Definition of body Euler angles with respect to the lab frame. \hat{x}_b is the long body axis. (c) Definition of Euler angles and body frame ($\hat{x}_b, \hat{y}_b, \hat{z}_b$). Wing angles are measured in the body frame with respect to the stroke plane (shaded blue, SI). (d) Top and side-views of 10 consecutive wing-strokes of the maneuver, taken when the wings are at their forward-most position. The perturbation wing-beat is numbered 0. (e) The body Euler angles during the maneuver. The perturbation was applied between 0–5ms (yellow). White and gray stripes represent forward and back strokes, respectively. Yaw and pitch were sampled at 8000Hz. Roll was measured manually at the middle of each half-stroke and smoothed by a spline (dashed line). Measurement errors are comparable to the symbols size.

tween $t = 0 - 5\text{ms}$ and induced a maximum roll velocity of 7000°s^{-1} resulting in a deflection of 60° within $t = 13.5\text{ms}$ (Frame 3, Fig. 1d). The fly recovered its initial roll angle within 35ms, or 8 wing-beats. Top views show a clear asymmetry in wing stroke angles during the maneuver, which starts a single wing-beat (5ms) after the perturbation (Fig. 1d, frames 1–4). During the maneuver the left wing stroke amplitude increases while

the right wing stroke amplitude decreases. The fly also spreads its legs from their folded position (frames 4–8) as in a typical landing response [41–43]. In addition, smaller deflections of 25° left in yaw and 5° down in pitch were induced, since the applied torque is not completely aligned with a principal body axis (Fig. 1e, SI).

We quantify the asymmetry in wing kinematics by plotting the wing stroke angles during the maneuver (Fig. 2a). We find large differences – up to 70° – between their peak-to-peak amplitudes (Fig. 2b, SI). The amplitude asymmetry began 1 wing-beat after the onset of the perturbation, and lasted for 5 wing-beats. The flapping frequency of both wings remained nearly constant during the maneuver. Hence, to maintain the amplitude asymmetry, the right wing moved faster than the left (Fig. 2c). To first order, this difference in velocity leads to asymmetry in the aerodynamic forces of the two wings and generates a correcting torque.

To calculate the aerodynamic torque generated by the insect, we used the full measured wing and body kinematics combined with a quasi-steady-state model for the aerodynamic force [44] produced by each wing (SI). The calculated torques are similar for other quasi-steady-state force models [45, 46] as well. The components of the aerodynamic torque vector along the \hat{x}_b and \hat{z}_b body axes were averaged over half-strokes and plotted in Fig. 2d,e (see Fig. 1c for axes definition). The torque magnitude is roughly $5\text{nN} \cdot \text{m}$ and is comparable to torques exerted by tethered fruit flies [23]. Both the \hat{x}_b and \hat{z}_b torque components have a corrective effect along roll, and both exhibit distinct peaks (solid circles) that appear simultaneously with the stroke-amplitude asymmetry. Our calculations also show that passive roll damping is too weak to explain the observed maneuver (SI).

This amplitude asymmetry can be described by the response of a linear, proportional-integral (PI) controller:

$$\Delta\Phi(t) = K_p\dot{\rho}(t - \Delta T) + K_i\rho(t - \Delta T). \quad (1)$$

Here, the output $\Delta\Phi$ is the difference between the right and left wing stroke amplitudes, and the controller's input is the body roll velocity, $\dot{\rho}$, which flies measure using their gyroscopic sensor system associated with the haltere organs [20, 47, 48]. The controller is defined by three parameters: the proportional gain K_p , the integral gain K_i , and a delay ΔT that describes the neuro-muscular response time. Fitting these three parameters using the measured $\dot{\rho}$, ρ and $\Delta\Phi$ (Fig. 2f), we find this controller response (red curve) is sufficient to reproduce the time-dependence of $\Delta\Phi$ (green circles). Moreover, the fast rise time can be attributed to the term proportional to the roll velocity (blue curve). Simpler models, such as I- and P-controllers, can be excluded (SI). As such, this PI model is the simplest continuous linear control mechanism consistent with our observations.

The salient correction feature – a wing stroke amplitude asymmetry with a delay of ~ 1 wing-beat – was observed in all the recorded events (Fig. 3a). Moreover, this feature was robust to variability in initial flight pose

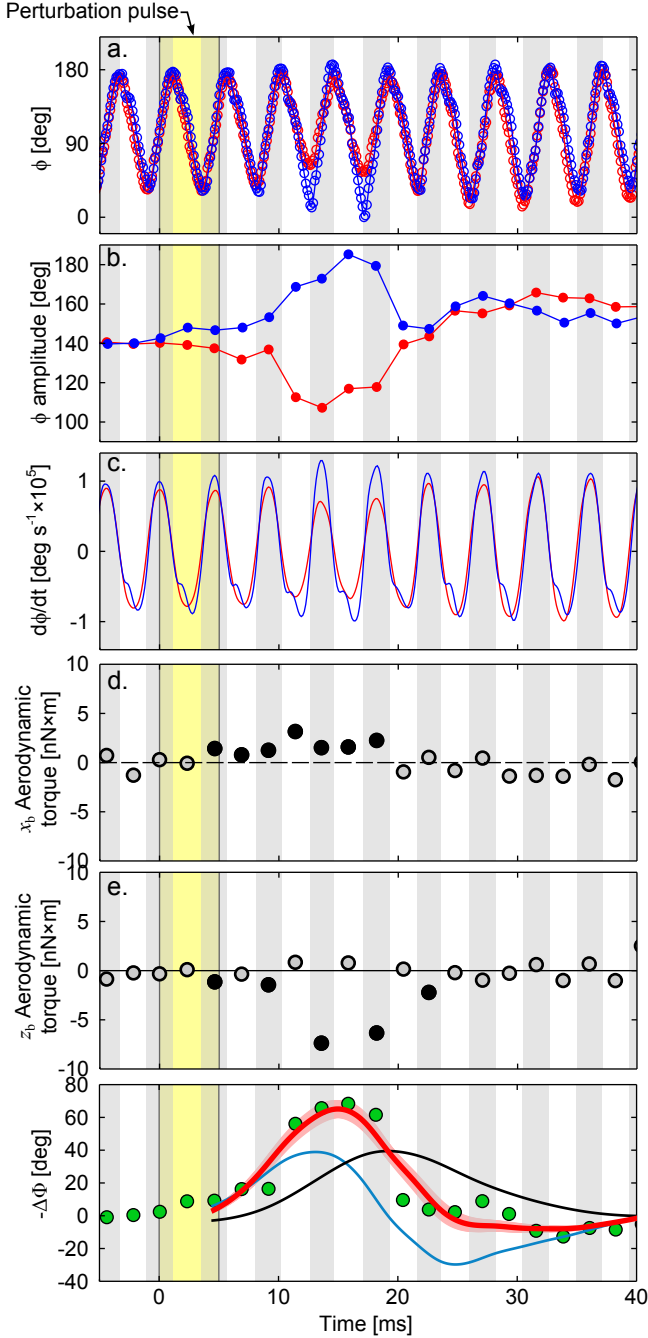


FIG. 2. Roll correction mechanism for the correction maneuver shown in Fig. 1. (a-c) Wing stroke kinematics versus time: (a) The stroke angle ϕ of the right (red) and left (blue) wings; (b) their peak-to-peak amplitude Φ , and (c) their angular velocity $\dot{\phi}$ (c). (d-e) Mean aerodynamic torque along each half stroke, calculated from the measured wing kinematics using a quasi-steady state aerodynamic force model. Solid symbols highlight the correcting wing strokes. (d) the torque component along the body axis \hat{x}_b . Positive torque induces a corrective right roll; (e) The torque component along \hat{z}_b . Negative values have corrective effect. (f) Wing stroke amplitude difference $\Delta\Phi$ (green), and a fit for a PI controller (eq. 1, red), with $\Delta T = 4.4 \pm 0.25\text{ms}$, $K_p = 6 \pm 0.5\text{ms}$, and $K_i = 0.7 \pm 0.05$ (fitted values \pm confidence intervals, shaded red, SI). Contributions of the 1st and 2nd terms of Eq. 1 are shown in blue and black, respectively. Measurement errors in (a-f) are comparable to the symbols size.

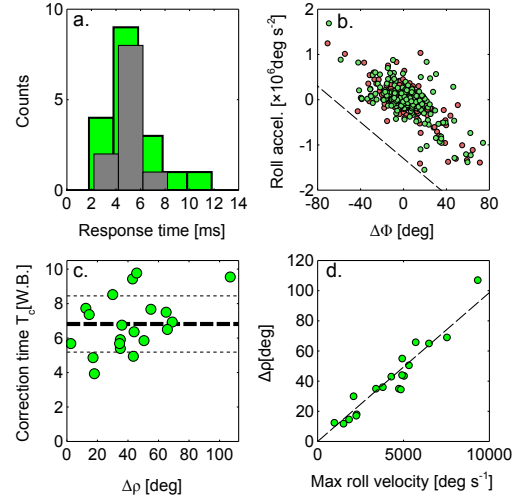


FIG. 3. (a) Response time histograms for multiple perturbation events: Delay time of fitted PI controllers (dark gray) and the time to reach $\Delta\Phi = 10^\circ$ measured from wing kinematics (green). Histograms are shifted to improve visibility. (b) Mean roll acceleration versus $\Delta\Phi$ for 299 forward strokes (red) and 304 back strokes (green). The correlation coefficient of these two quantities is -0.67 (p -value $< 10^{-12}$). The dashed line has a slope of $-20 \cdot 10^3 \text{s}^{-2}$. (c) Roll correction time T_c measured in wing-beats as a function of $\Delta\rho$ for multiple events. The mean correction time (thick dashed line) is 6.8 ± 1.6 wing-beats (mean \pm standard deviation). Thin dashed lines indicate 1σ margins. (d) Maximum roll displacement $\Delta\rho$ as a function of the maximum roll angular velocity for multiple events. The dashed line has a fitted slope of 9.9ms with a 95% confidence interval of $\pm 0.75\text{ms}$.

and velocity (Movies 2,3) and observed even for two consecutive perturbation pulses (Movie 4, Figs. S2,3). In-depth analysis of 11 correction maneuvers showed the $\Delta\Phi$ response is consistent with the PI controller model (fit mean $R^2 = 0.86$). Fitting control parameters for each maneuver separately, we find $K_p = 4.8 \pm 2.4\text{ms}$ and $K_i = 0.6 \pm 0.3$ (mean \pm standard deviation). The mean response time $\Delta T = 4.6 \pm 1\text{ms}$ is comparable to a single wing-beat period (Fig. 3a). The confidence intervals for parameters in each event are smaller than standard deviation, indicating differences between fitted controllers can be attributed to natural variation between flies (SI).

This response time is 3.5 times faster than the flies' response to yaw perturbations [32] and 2.5 times faster than their response to pitch perturbations [13]. The roll response is also 5 times faster than visual startle response in flies (25ms) [49] and is completed before they can elicit a visual response. In fact, this ability to respond within 5ms, places this reflex among the fastest in the animal kingdom, comparable to those in blowflies (5 – 7.5ms) [24], teleost fish (5 – 10ms) [40, 50], trap-jaw ants (4 – 10ms) [51] and cockroaches (11 – 18ms) [52, 53].

To further illustrate that wing asymmetry generates corrective roll dynamics, we determine the mean roll acceleration for ~ 600 half-strokes and plot it versus $\Delta\Phi$

(Fig. 3b, SI). The $\Delta\Phi$ asymmetry is negatively correlated with the roll acceleration generated by the fly. Thus, for example, negative $\Delta\Phi$ is correlated with positive roll acceleration (Figs. 1,2,S2,S3). The data also show two hallmarks of linear control. First, the correction time is insensitive to the maximum roll deflection, $\Delta\rho$. Here, the correction time T_c is the time between onset of the perturbation and the moment when the roll angle reaches 10% of $\Delta\rho$. Plotting T_c as a function of $\Delta\rho$ shows the correction time is 6.8 ± 1.6 wing beats (mean \pm SD, $n = 20$) with little dependence on perturbation amplitude (Fig. 3c). Second, we find $\Delta\rho$ increases linearly with maximum roll velocity (Fig. 3d). Collectively, these data suggest that as with yaw [32], the response to roll perturbations is well described by a reduced order model of a linear PI controller with time delay.

To test the linear control model we challenged the flies with extreme perturbations in which they were spun multiple times in mid air by a series of magnetic pulses. The fly shown in Fig. 4a and Movie 5 was rotated 8 times to its right. The accumulated roll angle exceeded 3000° (Fig. 4b) and the maximum roll velocity was over $60,000^\circ\text{s}^{-1}$ (Fig. 4c). During the perturbation, the fly was unable to oppose the magnetic torque. We captured 3 such events, all showing the same behavior. Remarkably, once the magnetic pulses stopped, the flies regained control within 3 – 4 wing-beats. Our calculations show roll deceleration is only explained by active flapping, rather than passive damping due to the wings (SI).

If the fly's roll controller were a linear PI (Eq. 1), the integral term should have accumulated a signal corresponding to a 3000° deflection. The resulting correction maneuver would require the fly to rotate 3000° in the opposite direction. Clearly flies circumvent this scenario by employing something like an integral “anti-windup” operation that prevents such accumulations from taking place. It is plausible that in such maneuvers the time scales are long enough that flies incorporate an additional sensory modality to determine the direction of gravity and do not rely on integration of angular velocity. Either way, the observed behavior is an example of a nonlinear feature for roll control during extreme perturbations.

We observed an additional nonlinear control feature that arose because the perturbing torque was not perfectly aligned with a principle body axis and induced secondary deflections along the yaw and body velocity directions. In contrast to previous experiments where perturbations were restricted to yaw and were corrected with small errors [32], here we observed that the secondary deflections along the yaw and body velocity orientations were often left partially uncorrected (Figs. 4de). For example, even after the roll correction, deflections at $t = 11$ wingbeats show yaw “errors” larger than 10% of the initial yaw perturbation (above the green region in (Fig. 4d) and body velocity orientation “errors” that are even larger than the initial body velocity orientation perturbation (orange area in Figs. 4e). The qualitatively different yaw response with and without the roll deflection hints

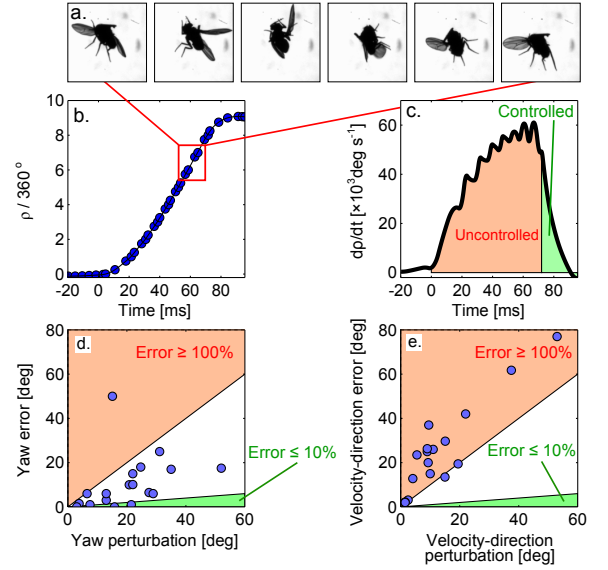


FIG. 4. Extreme perturbation. (a) Snapshots, taken 1.25ms apart, of a fly being rotated at $\sim 60,000^\circ\text{s}^{-1}$ by a pulse train of magnetic torques. (b) Roll kinematics during the maneuver (blue circles), and its smoothing spline (black line). The perturbation was on between $t = 0 - 72\text{ms}$. Measurement errors are smaller than the symbol size. (c) Roll velocity versus time (black line). The fly was unable to control its flight during the perturbation (orange shading) and actively corrected roll once the perturbation stopped (green shading). The fly leveled itself to $\rho = 20^\circ$ within 4 wing-beats after the perturbation stopped, towards $\rho = 0$. (d) Yaw difference between $t = 0$ and $t = 11$ wing-beats as a function of the maximum yaw perturbation. (e) A similar plot for the velocity heading.

that the fly prioritizes roll correction while compromising other angles. Such prioritization would require a control mechanism with nonlinear coupling of the body angles.

Collectively, these results shed light on important aspects of the fly controller. First, the flies' response to extreme perturbations of multiple roll rotations indicates they employ a nonlinear mechanism such as integral “anti-windup”. Second, their response to combined perturbations along multiple axes suggests their coupled control mechanism is hierarchical and therefore nonlinear, prioritizing roll - an unstable degree of freedom - while compromising other angles. Consequently, mapping out the architecture and hierarchy of the full controller will necessitate measurement of the insect's response to sophisticated perturbations along multiple axes, whose direction, amplitude and timing are individually controlled. Finally, the rapid response time of 5ms underscores the importance of roll control for flight. In addition, this small time scale suggests the neural circuit governing the response must be simple, consisting of only a few neural synapses between the haltere organs and the steering muscles. We envision that this simplicity opens the door to combined bottom up neuroscience experiments and top down biolocomotion studies, such as those presented here, aimed at elucidating the func-

tion of each neuron in the control circuit of this important model animal. Such measurements will further reveal the neural architecture behind the elegant strategies insects use to manage their actuation resources and achieve the grace and performance of their flight.

ACKNOWLEDGMENTS

Acknowledgments: T.B. was supported by the Cross Disciplinary Postdoctoral Fellowship of the Human Frontier Science Program. In addition the work was supported in part by an NSF-CBET award number 0933332 and an ARO award number 61651-EG. We thank Andy Ruina, Brian Leahy, Sagi Levy, Cole Gilbert, Ron Hoy, Paul Shamble, Jesse Goldberg, Sarah Iams, Leif Ristroph, Simon Walker, Svetlana Morozova, Noah Cowan, Brandon Hencey, Jen Grenier and Andrew Clark. Finally, T.B. would like to thank Anat B. Gafen for her invaluable support.

-
- [1] S. A. Combes and R. Dudley, Proceedings of the National Academy of Sciences **106**, 9105 (2009).
 - [2] S. Ravi, J. D. Crall, A. Fisher, and S. A. Combes, The Journal of experimental biology **216**, 4299 (2013).
 - [3] V. M. Ortega-Jimenez, J. S. Greeter, R. Mittal, and T. L. Hedrick, The Journal of experimental biology, jeb (2013).
 - [4] J. Vance, I. Faruque, and J. Humbert, Bioinspiration & biomimetics **8**, 016004 (2013).
 - [5] S. P. Sane, The Journal of experimental biology **206**, 4191 (2003).
 - [6] Z. J. Wang, Annu. Rev. Fluid Mech. **37**, 183 (2005).
 - [7] G. K. Taylor and A. L. Thomas, Journal of Experimental Biology **206**, 2803 (2003).
 - [8] M. Sun and Y. Xiong, The Journal of experimental biology **208**, 447 (2005).
 - [9] G. K. Taylor and R. Żbikowski, Journal of The Royal Society Interface **2**, 197 (2005).
 - [10] M. Sun, J. Wang, and Y. Xiong, Acta Mechanica Sinica **23**, 231 (2007).
 - [11] H. Liu, T. Nakata, N. Gao, M. Maeda, H. Aono, and W. Shyy, Acta Mechanica Sinica **26**, 863 (2010).
 - [12] I. Faruque and J. S. Humbert, Journal of theoretical biology **264**, 538 (2010).
 - [13] L. Ristroph, G. Ristroph, S. Morozova, A. J. Bergou, S. Chang, J. Guckenheimer, Z. J. Wang, and I. Cohen, Journal of The Royal Society Interface **10** (2013).
 - [14] N. Gao, H. Aono, and H. Liu, Journal of Theoretical Biology **270**, 98 (2011).
 - [15] B. Liang and M. Sun, Journal of The Royal Society Interface **10** (2013).
 - [16] N. Xu and M. Sun, Journal of theoretical biology **319**, 102 (2013).
 - [17] Y. Zhang and M. Sun, Acta Mechanica Sinica **26**, 175 (2010).
 - [18] M. Sun, Rev. Mod. Phys. **86**, 615 (2014).
 - [19] G. Nalbach, Neuroscience **61**, 149 (1994).
 - [20] M. H. Dickinson, Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences **354**, 903 (1999).
 - [21] A. Sherman and M. H. Dickinson, Journal of experimental biology **207**, 133 (2004).
 - [22] A. Sherman and M. H. Dickinson, Journal of Experimental Biology **206**, 295 (2003).
 - [23] H. Sugiura and M. H. Dickinson, PloS one **4**, e4883 (2009).
 - [24] R. Hengstenberg, D. Sandeman, and B. Hengstenberg, Proceedings of the Royal society of London. Series B. Biological sciences **227**, 455 (1986).
 - [25] M. V. Srinivasan, Journal of comparative physiology **119**, 1 (1977).
 - [26] B. Waldmann and W. Zarnack, Biological cybernetics **59**, 325 (1988).
 - [27] F.-O. Lehmann *et al.*, The Journal of experimental biology **201**, 385 (1998).
 - [28] J. Zanker, Philosophical Transactions of the Royal Society of London. B, Biological Sciences **327**, 43 (1990).
 - [29] S. P. Windsor, R. J. Bomphrey, and G. K. Taylor, Journal of The Royal Society Interface **11**, 20130921 (2014).
 - [30] S. N. Fry, R. Sayaman, and M. H. Dickinson, Journal of Experimental Biology **208**, 2303 (2005).
 - [31] J. A. Bender and M. H. Dickinson, The Journal of experimental biology **209**, 3170 (2006).
 - [32] L. Ristroph, A. J. Bergou, G. Ristroph, K. Coumes, G. J. Berman, J. Guckenheimer, Z. J. Wang, and I. Cohen, Proceedings of the National Academy of Sciences **107**, 4820 (2010).
 - [33] K. Tanaka and K. Kawachi, Journal of Experimental Biology **209**, 4533 (2006).
 - [34] C. F. Graetzel, B. J. Nelson, and S. N. Fry, Journal of The Royal Society Interface, rsif.2010.0040 (2010).
 - [35] A. Hyslop, H. G. Krapp, and J. S. Humbert, Biological cybernetics **103**, 353 (2010).
 - [36] N. Rohrseitz and S. N. Fry, Journal of The Royal Society Interface **8**, 171 (2011).
 - [37] B. Cheng, X. Deng, and T. L. Hedrick, The Journal of Experimental Biology **214**, 4092 (2011).
 - [38] B. Schnell, P. T. Weir, E. Roth, A. L. Fairhall, and M. H. Dickinson, Proceedings of the National Academy of Sciences **111**, 5700 (2014).
 - [39] L. Ristroph, G. J. Berman, A. J. Bergou, Z. J. Wang, and I. Cohen, Journal of Experimental Biology **212**, 1324 (2009).
 - [40] R. C. Eaton, *Neural mechanisms of startle behavior* (Springer, 1984).
 - [41] L. J. Goodman, Journal of Experimental Biology **37**, 854 (1960).
 - [42] A. Borst, Biological cybernetics **54**, 379 (1986).
 - [43] F. Van Breugel and M. H. Dickinson, The Journal of experimental biology **215**, 1783 (2012).

- [44] M. H. Dickinson, F. O. Lehmann, and S. P. Sane, *Science* **284**, 1954 (1999).
- [45] S. P. Sane and M. H. Dickinson, *Journal of Experimental Biology* **205**, 1087 (2002).
- [46] G. J. Berman and Z. J. Wang, *Journal of Fluid Mechanics* **582**, 153 (2007).
- [47] J. Pringle, *Royal Society of London Philosophical Transactions Series B* **233**, 347 (1948).
- [48] G. Nalbach, *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* **173**, 293 (1993).
- [49] H. Fotowat, A. Fayyazuddin, H. J. Bellen, and F. Gabbiani, *Journal of neurophysiology* **102**, 875 (2009).
- [50] R. C. Eaton, R. A. Bombardieri, and D. L. Meyer, *Journal of Experimental Biology* **66**, 65 (1977).
- [51] W. Gronenberg, *Journal of comparative physiology. A, Sensory, neural, and behavioral physiology* (1995).
- [52] J. M. Camhi and T. G. Nolen, *Journal of comparative physiology* **142**, 339 (1981).
- [53] D. L. Jindrich and R. J. Full, *Journal of Experimental Biology* **205**, 2803 (2002).